

Helminth Infections in the Townsend's Ground Squirrel during Drought

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ABSTRACT: From February to June 1992, 117 Townsend's ground squirrels (*Spermophilus townsendii*) were collected for necropsy on 11 open and 10 shrubby sites at the Snake River Birds of Prey Area, Ada County, Idaho. Cumulative precipitation was well below the 50-yr mean during the study period. Four species of helminths were recovered during the study: *Hymenolepis citelli* (10%, 12 of 117), *Pterygodermatites coloradensis*, sensu Hall 1916, (5%, 6 of 117), *Syphacia citelli* (3%, 4 of 117), and *Spirura infundibuliformis* (2%, 3 of 117). *Hymenolepis citelli* was present on 8 of 11 (73%) of the more stressful open sites vs. 2 of 10 (20%) of the shrub sites. Prevalence of infection with *H. citelli* was not significantly different between the 2 site types. There were no significant differences in prevalence of infection between males and females or adults and juveniles for any helminth species. *Hymenolepis citelli* was present in all months sampled except June, but there was no significant increase or decrease in prevalence as the drought progressed. The other helminths were observed in 2 or fewer months. Only a single squirrel was infected with >1 helminth species. Each helminth species occurred in a unique region of the squirrel gut. Measurements are given for the first intact females of *P. coloradensis*, increasing the size ranges for females of this species.

KEY WORDS: helminths, Townsend's ground squirrel, *Spermophilus*, drought.

The Townsend's ground squirrel (*Spermophilus townsendii* Bachman, 1839) is a small, short-eared ground squirrel that is locally abundant in parts of the Great Basin (Rickart, 1987). It is an obligate hibernator and is only active from February to May or June in most years. The helminth parasites of the Townsend's ground squirrel have been examined by Jenkins and Grundmann (1973) and Leiby (1962) and the coccidia by Wilber et al. (1994).

In conjunction with a larger mark-recapture study, we collected animals for necropsy during the entire period of squirrel activity (February to June) in 1992 at the Snake River Birds of Prey Area (SRBPA) near Boise, Idaho. Throughout the study, cumulative precipitation in the region was significantly below the 50-yr (1940–1990) mean (Fig. 1A); 1992 was the third driest year on record since 1900 (National Weather Service, Boise). In addition, mean maximum daily temperatures per month were above the 50-yr mean (Fig. 1B) (National Weather Service, Boise).

During the 4–5-mo active season, Townsend's ground squirrels (*Spermophilus townsendii*) accumulate body fat to allow survival during the

7–8 mo of dormancy they experience each year. In 1991 (a normal year), mean body masses of adults (averaged within weeks) increased about 50 g (20–28%) between 1 April 1991 and onset of dormancy. Juvenile body masses increased about 100 g (75–115%). In 1992, over the same time period, mean body masses of adult males and females declined (45 and 21%) while juveniles gained only 10–20% vs. 75–115% in 1991 (Van Horne, unpubl. data). Squirrel body masses were also grouped by age, sex, and site type (adult, juvenile, male, female, shrubby, open) and compared between 1991 and 1992, using an analysis of variance of body mass with day of year as a covariate. This analysis compared daily, not monthly, means and showed that body masses were significantly less in May 1992 than in May 1991 for adults and juveniles on open sites and for juveniles on shrubby sites (Table 1) (Van Horne, unpubl. data). Therefore, open sites seemed more stressful than shrubby sites. In addition to declines in body mass, recruitment was negatively affected. Eighteen percent (72 of 398) of juvenile males and 38% (169 of 444) of juvenile females PIT-tagged (Schooley et al., 1993) in the mark-recapture study in 1991 were recaptured in 1992. In 1992, 1,423 juveniles were PIT-tagged but only 9 (0.6%) were recaptured in 1993. Furthermore, total number of animals cap-

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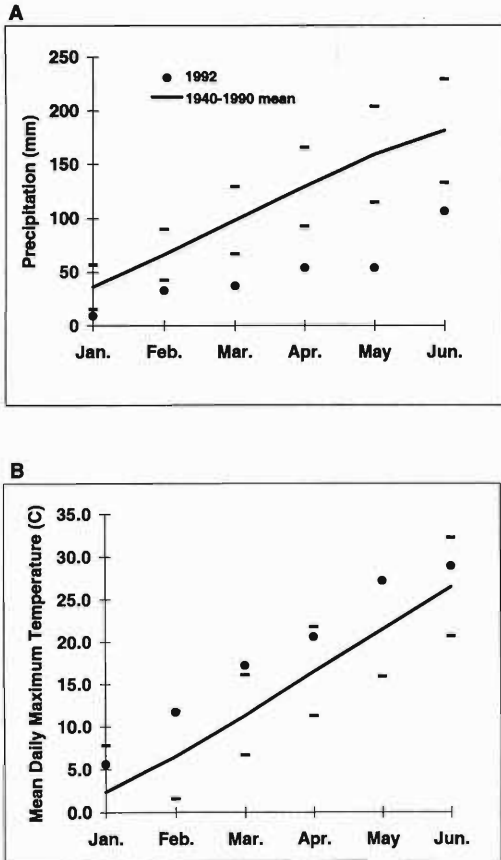


Figure 1. A. Cumulative precipitation encompassing the period of squirrel activity (February to June) in 1992 (dots) and for the 50-yr mean (1940-1990) (solid line) at the Boise Weather Station in Boise, Idaho, about 20 mi from the study site. The standard deviation for the 50-yr mean is indicated by the dashes. Note that the 1992 values are always below the lower limit of the standard deviation. B. Mean maximum daily temperatures (C) from January through June 1992 and for the 50-yr mean (1940-1990) at the Boise Weather Station in Boise, Idaho. Note that the maximum daily temperatures for 1992 are at or above the upper limit of the standard deviation 50% of the time and that all values in 1992 are above average.

tured in 1992 was 2,558 whereas only 872 animals were captured in 1993, despite an 18% increase in trapping effort in 1993 (68,068 trap sets) (Van Horne, unpubl. data). These data demonstrate that there was a drought in 1992 at the SRBPA during the period of squirrel activity and that this drought had a serious negative impact on squirrels. A drought, with similar effects on the Townsend's ground squirrels, was docu-

Table 1. The helminth work was a subset of a larger mark-recapture study. Data from the larger study was used to determine the effects of drought on squirrel body mass. An ANOVA was performed, with day of year as a covariate, to compare body weights at last capture for adult male, adult female, juvenile male, and juvenile female Townsend's ground squirrels (*Spermophilus townsendii*) on 2 site types (open and shrubby) in May 1991 vs. May 1992 (Van Horne, unpubl. data). This analysis compares daily, not monthly, means, so means are not included. Sample size, *F* value, and *P* value are presented.

Site	Age	Sex	<i>n</i>	<i>F</i> value	<i>P</i> value
Shrub	Adult	Male	51	0.10	0.7483
	Adult	Female	44	0.00	0.9846
	Juvenile	Male	150	49.96	0.0001
	Juvenile	Female	195	52.51	0.0001
Open	Adult	Male	58	47.83	0.0001
	Adult	Female	147	57.59	0.0001
	Juvenile	Male	232	19.07	0.0001
	Juvenile	Female	241	30.39	0.0001

mented at the SRBPA in 1977 (Smith and Johnson, 1985).

Many authors, including Esch et al. (1975) and Scott (1988), have suggested that decline in nutritional status of the host may result in increased prevalence of disease and parasitism in a host population and/or increased intensity of parasites in individual hosts. However, a relationship between nutritional status and parasitism is not well documented in wild rodents and only poorly documented in wild populations in general. We examined helminth parasites in Townsend's ground squirrels during the drought in 1992.

We compared helminth infections in squirrels living on open vs. shrubby sites and examined some of the biotic and abiotic factors affecting the structure of the helminth community in Townsend's ground squirrels. We present measurements for the first intact females of *Pterygodermatites coloradensis* sensu Hall, 1916.

Materials and Methods

Field collections

Between February and June 1992, 1 adult squirrel per month, as available, was collected for necropsy at the SRBPA near Boise, Idaho, from each of 10 open sites ($n = 37$) dominated by the grass *Poa segunda* and each of 10 shrubby sites ($n = 20$) dominated by big sage (*Artemisia tridentata*), winterfat (*Ceratoides lanata*), or a combination of the 2 shrubs. In May 1991, open sites averaged $0.3 \pm 0.4\%$ shrub cover while shrubby sites averaged $26.1 \pm 9\%$ shrub cover (Van Horne, unpubl. data). Sites ranged in size from 1 to

Table 2. The number of Townsend's ground squirrels (*Spermophilus townsendii*) infected with helminths each month, followed by prevalence and mean intensity of infection for all helminths recovered from the necropsy of 117 squirrels at the Snake River Birds of Prey Area near Boise, Idaho, in 1992.

Month	N	<i>Hymenolepis citelli</i>		<i>Syphacia citelli</i>		<i>Pterygodermatites coloradensis</i>		<i>Spirura infundibuliformis</i>	
		Infected (%)	Mean intensity	Infected (%)	Mean intensity	Infected (%)	Mean intensity	Infected (%)	Mean intensity
February	20	4 (20)	16.5	1 (5)	6	0	0	0	0
March	23	2 (9)	3	0	0	0	0	0	0
April	32	1 (3)	2	0	0	0	0	0	0
May	37	5 (14)	4.2	3 (8)	86.3	6 (16)	9.2	2 (5)	1
June	5	0	0	0	0	0	0	1 (20)	1
Total	117	12 (10)	7.9	4 (3)	66.3	6 (5)	9.2	3 (2)	1

9.5 ha. Twelve adult squirrels were obtained in February from an additional open site (nearly devoid of shrubs) for which exact cover information was not obtained. One juvenile per site per month was collected from the same sites following juvenile emergence (early April) until immergence in June ($n = 20$, open; $n = 28$, shrub).

Captured animals were transported to the field laboratory where they were euthanized with Halothane within 8 hr of capture. Blood for direct blood smears was drawn immediately after death via cardiac puncture. Blood smears were air-dried and carcasses were bagged and frozen within 5 min of death. Microslides and carcasses were transported to The University of New Mexico in June 1992 for analyses.

Laboratory procedures

Blood smears were fixed in absolute methanol, and stained with Giemsa-Wright. All slides were examined by a single observer for at least 10 min under oil immersion at $\times 1,250$ using a Leica microscope.

For necropsy, animals were thawed and the entire gastrointestinal tract was removed. The stomach and cecal contents were examined separately using the same methods. Contents were washed through a 40-gauge (0.425-mm) sieve, transferred to a petri dish, and examined under a dissecting scope at $\times 20$ or $\times 30$. Presence of arthropod parts in the stomach was recorded, but no identifications were made. The stomach and cecal tissues were also examined. The small and large intestines were slit longitudinally, and tissue and contents were examined under a dissecting microscope.

The location of all helminths within the gastrointestinal tract was recorded, and then worms were fixed in 10% buffered formalin for 24 hr. Nematodes were transferred to 70% EtOH with 3% glycerol and examined using lactophenol wet mounts under both dissecting and compound microscopes. Detailed measurements of morphologically intact *P. coloradensis* were made using a Zeiss compound microscope at various magnifications following Lichtenfels (1970). All measurements are in micrometers unless otherwise stated. Cestodes were stained with either Grencher's borax carmine, Ehrlich's hematoxylin, or Delafield's hema-

toxylin and permanently mounted in Canada balsam for examination.

The prevalence of infection for each helminth over the entire season in shrubby vs. open sites, males vs. females, and juveniles vs. adults was compared using Fisher's exact test ($P > 0.05$) (Mehta and Patel, 1992), but sample sizes for all helminths was low. We also determined prevalence and mean intensity of infection for each worm by month (Table 2). We used linear regression to determine whether or not there were any time-related trends in prevalence and intensity for *Hymenolepis citelli* (McLeod, 1933), the only parasite found in > 2 mo. We excluded infections in adults from shrubby sites ($n = 1$; captured 17 March 1992; infected with 1 tapeworm) from the regression analysis because adults on the shrubby sites were less severely affected by the drought than juveniles on shrubby sites and all animals on open sites (Table 1).

Voucher specimens of the helminth species recovered were deposited with the U.S. National Parasite Collection (USNPC), Beltsville, Maryland.

Results

No blood parasites were observed in the squirrels we examined, but 4 helminth species, all of which are new host records, were found (Table 2). Despite freezing of carcasses prior to necropsy, helminths were intact and easily identified and measured. Furthermore, location within the gastrointestinal tract for each species was consistent with locations described for these species in other hosts.

Hymenolepis citelli (McLeod, 1933) USNPC No. 83939

Prevalence and intensities are given in Table 2. Range of intensity was 1–41. There were no significant differences between prevalences of tapeworm infections for male vs. female or adult vs. juvenile Townsend's ground squirrels. *Hy-*

menolepis citelli did occur on significantly more of the open sites than shrubby sites (8 of 11 [73%] open sites vs. 2 of 10 [20%] shrub sites, $P = 0.03$), but prevalence of infection in the squirrel populations was not significantly different between the 2 site types (10 of 69 [14%] of squirrels on open sites vs. 2 of 46 [4%] on shrub sites, $P = 0.12$). There were no significant temporal trends for prevalence or intensity of infection. We excluded the single adult from a shrub site that was infected with *H. citelli* from this analysis.

***Pterygodermatites coloradensis* sensu Hall, 1916,
USNPC No. 83941**

Prevalence and intensities are given in Table 2. Range of intensity was 6–22. There were no significant differences between prevalences of infection for shrub vs. open sites, males vs. females, or adults vs. juveniles. Temporal trends were not analyzed because *P. coloradensis* was observed only in May (Table 2).

***Syphacia citelli* Tiner and Rausch, 1950,
USNPC No. 83940**

Prevalences and intensities are given in Table 2. Range of intensity was 6–119. There were no significant differences between prevalences of infection for adults vs. juveniles, males vs. females, or shrub vs. open sites. Temporal trends were not analyzed because worms were only detected in 2 mo.

***Spirura infundibuliformis* (McLeod, 1933)
USNPC No. 83942**

Prevalence and intensities are given in Table 2. No statistical comparisons were performed because only 3 individuals were infected and intensity was always 1. Only immature female worms were present.

Discussion

Three species of helminths have been reported from the Townsend's ground squirrel: *Citellina triradiata* Hall, 1916; *Physaloptera massino* Schultz, 1928 (Jenkins and Grundmann, 1973); and *Syphacia eutamii* Tiner, 1948 (Leiby, 1962). We did not recover any of these species; all 4 helminths we collected were new host records. We did not observe any parasites in the blood smears.

The original description of *Pterygodermatites coloradensis* by Hall (1916) was based on 2 males and a partial female taken from the chipmunk

Tamias quadrivittatus (Say, 1823) in Colorado. The parasite was then redescribed by Tiner (1948) using 9 females and 2 males recovered from 3 species of *Peromyscus*. Lichtenfels (1970) reviewed this genus and suggested that the specimens collected by Tiner (1948) were distinct from those described by Hall (1916), and he renamed Tiner's specimens *Pterygodermatites peromysci* (Tiner, 1948) while the worms described by Hall retained the name *P. coloradensis*. Unfortunately, although many authors have reported this nematode from rodents, few have deposited their specimens in an accredited national repository. Thus, Lichtenfels (1970) was forced to base his redescription on only 3 specimens: 1 male and 2 partial females, 1 mature and 1 immature.

Pterygodermatites coloradensis has previously been described from only 1 species of ground squirrel, *Spermophilus variegatus* (Erxleben, 1777) (Jenkins and Grundmann, 1973). However, it has been reported from several other sciurids, *Tamias amoenis* Allen, 1890 (Rankin, 1945); *Tamias palmeri* (Merriam, 1889) (Archie et al. 1988); the antelope ground squirrel (no scientific name given) (Grundmann, 1957); and *Ammospermophilus leucurus leucurus* (Merriam, 1889) (Jenkins and Grundmann, 1973). It has also been reported from deer mice (*Peromyscus* spp.) (Rankin, 1945; Frandsen and Grundmann, 1959). This is the second observation from a spermophilid, and we present averages and size ranges for 11 males and 14 complete females. Our measurements of males are in close agreement with those of Lichtenfels (1970), with minor extensions of the size range (Table 3). The size range for many of the characters of the females has been extended. General morphological characteristics of the females were consistent with the description by Lichtenfels (1970). Because of the poor condition of the specimens available to Lichtenfels (1970), he was not able to determine the position of the vulva relative to the esophagus. We found that the vulva was posterior to the esophagus in the smallest females (9 mm) and anterior to the posterior end of the esophagus in females longer than 9 mm. In all cases, the vulva was between the 31st and 32nd pair of combs.

During our study in 1992, there was drought at the SRBPA (see the introduction). Based on comparisons of body masses between years (Table 1), open sites seemed the most stressful. If decreased nutritional status leads to an increase in parasitism (Esch et al., 1975; Scott, 1988),

Table 3. Measurements of *Pterygodermatites coloradensis* collected from Townsend's ground squirrels at the Snake River Birds of Prey Area near Boise, Idaho, in 1992 compared to those from Lichtenfels (1970).

	Males (N = 11)		Females (N = 14)	
	This study average (range)	Lichtenfels average	This study average (range)	Lichtenfels average
Total length (mm)	3.5 (3.0–4.0)	3.3	13 (9.0–17.0)	9 (est)*
Maximum diameter	277 (235–298)	277	448 (372–683)	360
Diameter base of buccal cavity	81 (70–89)	81.3	142 (120–174)	120
Buccal cavity depth/width	29/41 (24–35/35–50)	27/49	55/74 (50–65/65–89)	54/78
Esophagus length	1,044 (893–1,118)	875	2,152 (1,739–2,484)	1,500
Nerve ring from anterior	185 (180–223)	100	248 (200–310)	250
Largest comb height/width	45/99 (35–55/80–114)	45/85	48/105 (40–60/89–114)	42/105
Diameter of vulva	—	—	320 (285–397)	270
Vulva from anterior	—	—	2,074 (1,490–2,359)	—
Vulva from posterior	—	—	1,030 (675–1,491)	—
Egg length/width	—	—	42/30 (38–46/24–36)	38–40/22–24
Longest spine	—	—	92 (84–104)	81

* Estimated.

prevalence and intensity of parasitism should increase from February to June 1992 in juveniles on all sites and in adults on the open sites at the SRBPA, and infections should be more prevalent on open sites than on shrubby sites. We found no significant increase or decrease in the prevalence of infection for *H. citelli*, and there was no significant change in intensity during the drought (Table 2). Although the number of sites we compared was small and the proportions we obtained were only accurate to within 25% (Zar, 1984), significantly more open sites than shrubby sites harbored infected squirrels (8 of 11 [73%] open sites vs. 2 of 10 [20%] shrubby sites, $P = 0.03$). However, the prevalence of infection on open vs. shrubby sites was not significantly different (10 of 69 squirrels [14%] vs. 2 of 48 [4%], $P = 0.12$). The difference in distribution of *H. citelli* on open vs. shrub sites did not reflect differences in arthropod consumption rates by squirrels between the 2 site types; squirrels captured on open sites were significantly less likely to have arthropod parts in their gastrointestinal tracts than those captured on shrubby sites (16 of 69 [23%] vs. 20 of 48 [42%], $P = 0.04$). The species of arthropods that were consumed may be important, but arthropod parts were not identified.

The lack of temporal trends in prevalence and intensity of infection for *H. citelli* during the drought, and the lack of difference in prevalence of infection between the open (more stressful) and the shrubby sites suggests that either (H1) chance of infection with *H. citelli* was small

enough that the temporal effects of the drought were not observable with the samples sizes we collected or (H2) no temporal trends in the prevalence or intensity of *H. citelli* occurred. The current study does not allow us to distinguish between these 2 hypotheses.

Wilber et al. (1994) found a significant decrease in the prevalence of eimerian infections in 1992 in this same population of Townsend's ground squirrels, but an increase in the prevalence of gastric ulcers from February to April (Wilber, pers. obs.). Based on the varied temporal trends observed for *H. citelli*, eimerians, and gastric ulcers in the Townsend's ground squirrels at the SRBPA in 1992, we suggest that differences in parasite life-history parameters, immune responses of the host to the parasites, and abiotic effects on the parasites may interact to produce highly variable temporal responses to the same environmental perturbation.

Prevalence of infection with the tapeworm *H. citelli* at the SRBPA was similar to values reported in other spermophilids as was range of intensity (1–41) and average intensity (Table 2) (see Broda and Schmidt, 1978; Shults and Stanton, 1987).

Prevalence of *P. coloradensis* (Table 2) was not significantly different than the prevalence of 3% (1 of 54) in *S. variegatus* (Jenkins and Grundmann, 1973). Intensity and mean intensity could not be compared to other reports because no other data on intensity of *P. coloradensis* in spermophilid or ammospermophilids has been published.

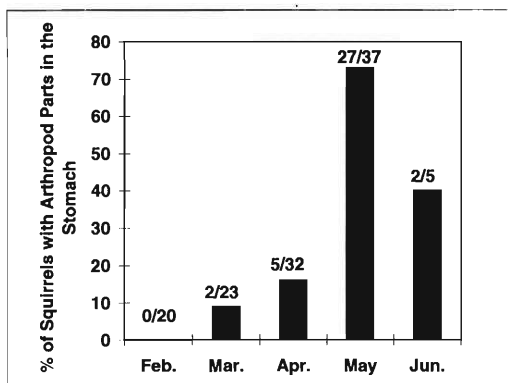


Figure 2. The percentage (%) of Townsend's ground squirrels (*Spermophilus townsendii*) ($N = 117$) collected at the SRBPA from February to June 1992 with arthropod parts in the gastrointestinal tract.

The low levels of infection with *P. coloradensis* early in the season may reflect a lack of suitable intermediate hosts in the environment, incomplete development of the intermediate stage in the arthropods, or low levels of consumption of arthropods by the squirrels from February to April (Fig. 2).

The prevalence of *S. citelli* in Townsend's ground squirrels ranged from 0 to 8% (Table 2), which is low compared to most other reports (see Jenkins and Grundmann, 1973; McGee, 1980; Shults and Stanton, 1987). The range of intensity (6–119) and average intensity (Table 2) were similar to previous reports.

Spirura infundibuliformis has been described from 3 species of ground squirrel and was re-described by Anderson et al. (1993). Prevalence of infection for *Spermophilus richardsonii* (Sabine, 1822) ranged from 7% in May to 100% in June, probably because the "local grasshoppers" (no scientific name given) that can serve as the intermediate host for this nematode became more abundant later in June (Anderson et al., 1993). Townsend's ground squirrels were also infected in May and June (Table 2) but prevalence and intensity (1 worm/squirrel) were low compared to those in other reports (McGee, 1980; Anderson et al., 1993).

There is general interest in understanding factors that structure helminth communities. In Townsend's ground squirrels at the SRBPA during the drought in 1992, only 1 of 117 squirrels was infected with > 1 species of helminth. Given the low prevalence of the helminths in 1992,

squirrels may have encountered infective stages so infrequently that the opportunity to acquire multiple infections was rare, thus the community structure was probably determined primarily by chance.

Interestingly, the 4 helminths occupied different regions of the gut: *S. infundibuliformis* was found only in the stomach, *P. coloradensis* only in the small intestine just below the pyloric sphincter, *H. citelli* only in the middle of the small intestine, and *S. citelli* only in the cecum. Possible overlap may occur between *P. coloradensis* and *H. citelli*, but the 2 worms were never observed to coexist. The use of different regions of the gut by the helminths may result in decreased competition when multispecies infections occur.

The helminth community in this sample of Townsend's ground squirrels consisted of 3 worms with indirect life cycles requiring arthropods and only 1 with a direct life cycle. In addition, *Dipodomys merriami* Mearns, 1890 (Merriam's kangaroo rat), at the Sevilleta National Wildlife Refuge near Socorro, New Mexico, had 10 helminths, 8 which require arthropods as the intermediate host and 2 with direct life cycles (Patrick, 1995). The predominance of helminths with indirect life cycles in these 2 arid environments contradicts Dobson's (1989) hypothesis that macroparasites with direct life cycles should be more common than those with indirect life cycles in arid regions. We suggest that parasites utilizing arthropods as intermediate hosts may be especially well adapted to xeric environments because arthropods tend to be abundant in deserts (McMahon, 1985) (facilitating infection of the arthropod by the parasite) and the intermediate host may provide a buffer against desiccation. Parasites in arid areas that have direct life cycles might be most effectively transmitted through direct contact between hosts, as may be the case for the cecal worms in both the kangaroo rats and the ground squirrels, or have eggs/propagules that are resistant to desiccation, as do eimerians. Seven species of *Eimeria* inhabit both Townsend's ground squirrels (Wilber et al., 1994) and Merriam's kangaroo rats (Patrick, 1995).

In summary, the Townsend's ground squirrel in Idaho during a drought was infected with 4 species of helminths, all of which were new host records. Three of these helminths have indirect life cycles and 1 has a direct life cycle, contra-

dicting Dobson's (1989) hypothesis. *Hymenolepis citelli* was more widely distributed among the more stressful open sites, but there were no differences in prevalence of infection between open and shrubby sites, and no temporal trends in the prevalence or intensity of this helminth were observed. Only 1 squirrel harbored a multispecies infection, and each helminth occupied a unique region of the gut.

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